BOMBARDIER BEETLES (COLEOPTERA, CARABIDAE) OF NORTH AMERICA: PART II. BIOLOGY AND BEHAVIOR OF BRACHINUS PALLIDUS ERWIN IN CALIFORNIA[1]

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Very little is known about the life history of bombardier beetles even though the group is plentifully represented in most parts of the world. Brief references have been made to the larvae of these interesting beetles, and the papers have dealt mostly with descriptions of first instar larvae of species of either *Brachinus* or *Pheropsophus*. In this paper I describe the immature stages of *Brachinus pallidus* Erwin, 1965, discuss the life history and behavior of these beetles, and review all available life history information concerning the bombardier beetles.

Wickham (1893:330) recorded the larval habits and parasitic relationships of *Brachinus* to water beetle pupae. He briefly described and illustrated the last instar larva and pupa of *B. janthinipennis* (Dejean).

Dimmock and Knab (1904:30) included Wickham's observations in their own publication on immature Coleoptera. Their work is much better known than that of Wickham's and they have erroneously been given credit in subsequent literature for the first discovery of *Brachinus janthinipennis* larvae.

A. de Orchymont (1920:59) noticed the similarities between the biology of *Lebia scapularis* Fourcroy and *B. janthinipennis* (Dejean) and predicted the existence of a free-living first instar for *Brachinus*.

Van Emden (1919:34) has described the first instar larva of *Pheropsophus* which were reared from eggs deposited by adults of *P. hispanicus* Dejean in the Canary Islands. Boldori later (1939:173) reared and described the larvae of *Pheropsophus africanus* Dejean. Boldori did not rear them beyond the first instar probably because of their special food requirements. Habu and Sadanaga (1965) described the first instar of *B. (Brachynidius) incomptus* Bates and worked out part of the life history of *Pheropsophus jessoensis* Morawitz. The descriptions are detailed and are accompanied by excellent illustrations. Jeannel (1942:1104) repeated Van Emden's description and reviewed those finds made by Wickham.

Recently, Wautier (1963) described the first instar larva of *Brachinus (Brachynidius) nigricornis* Gebler. This description is detailed and is accompanied by excellent illustrations.

In August of 1965, I discovered many pupae of the hydrophilid beetles *Tropisternus ellipticus* (Le Conte) and *Berosus punctatissimus* Le Conte under rocks near the Gilroy Hot Springs area of Coyote Creek, in Santa Clara County, California. Almost every one had a small larva adhering to it. These small larvae were reared, and developed into adults of *Brachinus pallidus* Erwin and *Brachinus fidelis* Le Conte. Subsequent intensive field work resulted in the discovery of many of the older instars of *Brachinus pallidus* in their natural habitat.

Shortly after these discoveries at Coyote Creek, Dr. Carl H. Lindroth informed the author *(in litt.)* that a larva of *Brachinus* had been found in Canada feeding on the pupa of a hydrophilid beetle. Based up on these three separate observa-

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tions (Wickham's, Erwin's, and Lindroth's), it is assumed that ectoparasitoidism[3] is obligatory for the post-embryonic development of at least the North American species of *Brachinus*. The entire life cycle of *Brachinus pallidus* will be discussed here, with descriptions and illustrations of all the immature instars.

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LIFE HISTORY AND GENERAL BIOLOGY

MATING—I observed pairs of *Brachinus pallidus* in coitus as early as May (in the laboratory) and as late as September (in the field). Mating was commonly observed throughout this period, occurring either at night or during the early morning hours, about dawn. Copulation usually takes place on top of a dry rock. The female beetle is mounted from the rear by the male which assumes the following position: fore-tarsi on the female pronotum, middle tarsi on the female elytral humeri and hind tarsi near the female elytral apices. The male's hind pair of legs rub the female's elytral apices during copulation. The antennae of both sexes are held straight forward, and the male's antennae palpitate the female's antennae during mating. In repose, the aedeagus of ground beetles is 90° counterclockwise from the true morphological position. As the aedeagus is extruded prior to copulation it rotates another ninety degrees counterclockwise, and is thus exactly upside down when fully extended. It is then directed forward under the male abdomen and enters the female genital chamber. The median lobe goes into the female as far as the parameres, which are small and are located at the base of the median lobe. It is not known whether the membranous apical sac, the endophallus of the aedeagus, completely inflates after insertion into the female genital chamber, but many authorities suspect that it does. The sclerotized tip of the endophallus, or virga (Snodgrass, 1939) is probably implicated in the copulatory process, but its exact function in *Brachinus* is not known. Actual intromission lasts only a few seconds, but the male remains mounted on the female for an hour or more if not disturbed.

OVIPOSITION—Within a few days after copulation the female oviposits in the gravel near the stream or pond. Just prior to oviposition the female beetle becomes quite excited in her movements, running rapidly over the rocks and gravel. When she encounters a slightly muddy spot she begins the process of gathering a mud ball on the tip of her abdomen. The last two abdominal segments are used as a scoop. With back and forth motions of the entire body, the female scrapes a small packet of mud from the wet rocks or soil. This process continues for at least four or five minutes, until she has enough mud to form a ball at the abdominal apex. The female then again runs rapidly over the rocks and gravel until she locates a small, damp stone that is laying on the gravel. With the valvulae the egg is pressed into the center of the wet ball of mud at the tip of the abdomen, then the encased egg is released onto the damp rock. The time required for this process varies between species. *Brachinus fidelis* Le Conte requires a full minute to oviposit, while *B. pallidus* needs but a few seconds. Oviposition takes place about dawn, just before the nocturnal adults retreat to

[3] Parasitoid is a term applied to parasites that normally cause the host to die in a short time.

cover for the day. A female lays two or three eggs a day for several days.

The eggs are ellipsoidal, with blunt ends. They are white and smooth, and have no hooks or spines. The mud ball enclosing the egg may be almost any shape, but is usually oval.

ECLOSION—Within a week after oviposition the first instar larva of *B. pallidus* chews its way out of the egg and through the mud wall surrounding the egg. There is no "egg burster" on these first instar larvae as there is in most other carabids. Even *Pheropsophus* has an egg burster consisting of a single median spine (Van Emden, 1942a), which may represent a stage between the typical condition in carabids toward that of total absence in *Brachinus*.

LARVAL DEVELOPMENT—The first instar larvae of *B. pallidus* are typically caraboid in shape and behavior. These first instar larvae begin their active search for a host immediately after eclosion.

It is necessary here to relate a partial life history of the species of beetles upon which the two species of *Brachinus* in this study feed. *Tropisternus ellipticus* (Le Conte) and *Berosus punctatissimus* Le Conte are Hydrophilidae with aquatic larvae, but both have terrestrial pupae. The larvae of these species crawl away from the water of the stream, through the coarse gravel, until reaching a site beside a boulder resting on soil or sand. There they stop and begin thrashing about. This activity eventually causes a small chamber to form in the damp soil or sand beneath the larva, and it then pupates in that cavity beside and partially beneath the boulder.

The actual feeding begins on the prosternum of the pupa. This results in a reddish appearance at the site of mandibular puncture which spreads rapidly over the dying pupa. Fifteen hours after feeding has begun the entire pupa is dark red. Within a few hours the first instar moults to the second instar, without moving from its meal. The second instar is quite unlike the first. A change in the mouth parts is evident, along with a shortening and thickening of the legs. The abdomen begins to take on a swollen appearance. A short time after the second instar begins to feed, the host pupa dies and begins to turn a very dark reddish color. The *Brachinus* larva then moults to the third instar and continues feeding at an even faster rate. The feeding proceeds from the prosternum inward and then posteriorly. The moult to the fourth instar occurs between the twentieth and thirtieth hour after the first instar began feeding. The fourth instar finishes devouring the pupal host and then moults to the fifth instar. The hydrophilid pupa has been completely consumed by that time and all that remains in the pupal chamber is the fifth instar *Brachinus* larva, which pupates four to five days later, still within the hydrophilid pupal chamber.

PUPATION—Pupation of *Brachinus pallidus* and *fidelis* takes place in the chamber which the hydrophilid host originally formed. The pupal stage of *Brachinus fidelis* requires only eight days to develop at room temperature and emerge as an adult beetle. Since there is barely a trace of the hydrophilid pupa left in the chamber, it might appear to the casual observer that the *Brachinus* larva had formed the chamber, as do some other carabids *(Agonum)* in the same area. However, observation of the entire sequence of events has made it obvious that this is not the case. The *Brachinus* larva simply replaces the hydrophilid pupa in its cell after devouring it.

The pupae of these two *Brachinus* species are white and have several long, stout dorsal hairs, which keep the body free of the damp substrate and may thus

protect it from becoming too wet. In all cases observed the pupae were supine in the chamber, supported on the long hairs. The *Brachinus* pupa begins darkening within three days after pupation occurs. The mandibles and eyes darken first, then the rest of the body turns a pale yellowish color. The new adults are totally white, except for the mandibles and the eyes which are black. Pigment deposition begins almost immediately and is complete in about four to six hours. Hardening of the cuticle requires several days or weeks to complete.

EXTERNAL MORPHOLOGY OF IMMATURE *Brachinus pallidus* ERWIN

The larvae of both *Brachinus pallidus* Erwin (and also *Brachinus fidelis* Le Conte) undergo two-stage polymorphic metamorphosis. The first instar larva is typically carboid except for the tarsunguloid legs, absence of a ligula, and short non-segmented urogomphi. The second through the fifth instar larvae have somewhat reduced legs and mouth parts and do *not* resemble normal caraboid larvae.

FIRST INSTAR LARVA (Photographs 1, 2).—The first instar larvae are about 3.2 mm in length, but the size varies somewhat, depending upon the size of the female that laid the egg. The head and thorax are distinctly sclerotized and pigmented, but the abdominal segments are soft and very lightly pigmented dorsally. Setae of various sizes and lengths occur both on the head capsule and the body. There are no egg busters as have most other carabids, thus it is probable that the larva simply chews its way out of the egg. *Head* (Plate 2, figures 1, 2). Head large and square, prognathus and depressed. Epicranial suture narrowly "U"-shaped, enclosing a fused frons and clypeus. Fronto-clypeal area modified into a nasale, which is rounded anteriorly and bears no teeth. Front piece barely convex. Cervical region slightly constricted and very short. Mandibles strong sickle-shaped, deeply pigmented and each with a small retinaculum at basal third. Antennae 4-segmented with first, third and fourth articles bearing long setae and third and fourth articles also bearing several sensory papillae. Third article dilated and bearing four of these small, knob-like sensory papillae; two located dorsally toward lateral lobe and two located ventrally below lateral lobe. Lateral lobe with a supplementary process resembling a small transparent bubble. Fourth article with three sensory papillae and four long setae, all of which are located terminally. Two distal sensory papillae of fourth article long and pencil-like, while the third papilla is spinelike and is located laterally at the base of the other two papillae. Labium (prementum) without a ligula but with a pair of 2-segmented palpi. Venter of labium bears two long setae. Dorsum of labium bears four short setae. Last article of each labial palpus bears two short ventral setae. Maxillae well developed, each with a basal cardo, a long curved stipes, a 4-segmented palpus and a long, ridged mala. Cardo with one ventrally located seta. Each stipes bears four setae, two of which are ventral-lateral and two on the mesal edge. Mala (a single apical lobe of maxilla, formed of the fused galea and lacinia) about two-thirds the length of the maxillary palpus and bears six setae and one anterior mesal sensory papilla. Each palpus with a ventral seta on first article, a dorsal seta on second article, and two ventral setae and one dorsal seta on third article. Organs of vision consist of six stemmata on each side of head capsule, arranged in two vertical rows of three per row. Stemmata located laterally, and caudad to base of mandibles. They are surrounded by darkly pigmented granules. *Thorax*. Prothorax at middle slightly broader than head and equal to it in length. *Legs* (Plate 3, figure 5). Legs twice as long as corresponding

thoracic segments are wide. *Abdomen.* Abdomen 10-segmented, with lightly pigmented dorsal sclerites. Urogomphi very short, unsegmented, and non-sclerotized, each bearing five long setae (one near base and four in a ring near apex). Pygopod (uropod, or tenth segment) well developed and divided terminally into two lobes (Plate 1, figure 3). This structure is well developed for locomotion and helps the larva adhere to the pupa it parasitizes.

SECOND INSTAR LARVA (Photograph 3).—The second instar larvae are about 4 mm in length, with the abdomen being very white and soft, and they have lost the typical caraboid appearance. Cephalic pigmentation is lacking, although there is faint sclerotization. *Head* (Plate 2, figures 3, 4). Head smaller in relation to body size than in first instar. It is more rounded, rather than being square. Epicranial suture "U"-shaped. Labrum and clypeus partially differentiated, thus not forming a true nasale. Frons flat, rather than convex. Cervical region of head constricted and very short. Head capsule with darkly pigmented lines near the cervix, but faintly sclerotized areas extend beyond these lines, gradually becoming membraneous posteriorly. The inflated body segments begin with the prothorax, making the head appear very small in proportion to the body. Mandibles reduced in length (compared to first instar mandible-head ratio). They are short and arcuate rather than being long and sickle-shaped. Small retinaculum present at basal third of mandible. Antennae 4-segmented, with third and fourth articles bearing long setae and sensory papillae. Third article with one lateral papilla and fourth with two apical papillae. Lateral lobe of third article with a supplementary process resembling a small knob, but it is not at all transparent (as it was in the first instar). Labium without ligula. Venter of labium with two short setae. Labial palpi each 2-segmented. Maxillae reduced in comparison with those of the first instar, but still well developed. Each maxilla consists of a cardo fused to a long, straight stipes. Each maxilla bears three dorsal and three ventral setae, and also with a small mesal spine adjacent to labium. A 4-segmented palpus and a long mala occur near the tip of each maxilla. Mala about two-thirds as long as maxillary palpus and with two apical setae and two apical sensory papillae. One seta also is visible on the third segment of maxillary palpus. Venter of head capsule with two tentorial pits near the center. Organs of vision are represented by six pigmented areas on each side of head, arranged in two vertical rows of three in a row (sometimes there are only five on the right side of the head). There are no definite functional stemmata, as there were in the first instar. Pigmented areas located laterally and caudad to each mandibular base. *Thorax.* Prothorax broader and slightly longer than head capsule. *Legs.* All legs very short, only about as long as head. *Abdomen.* Abdominal segments soft, and proportionally broader than in the first instar, and each segment also expanded into large white lobes ventrally. Urogomphi very short, non-segmented, and soft, each bearing five long setae (one basally and four actually on the urogomphus). Pygopod relatively shorter than on first instar, and modified in the second and subsequent instars into a short anal tube.

THIRD INSTAR LARVAE (Photograph 4).—Third instar larvae about 6 mm in length similar in form to second instar larvae. Cephalic pigmentation entirely lacking, although there is slight sclerotization. *Head* (Plate 2, figures 5, 6). Head smaller in proportion to body size than in previous instars, but resembles head of second instar by being rounded, rather than square. Epicranial suture "U"-shaped,

enclosing the fused labrum and clypeus. Frons and clypeo-labral areas fused into a single central lobe. Front slightly concave at sides rather than being flat. Cervical region of head constricted and short. All body segments are swollen, including the prothorax, making the head seem very small in proportion to the rest of the body. Mandibles even more reduced than in second instar, being very short and stubby rather than long and sickle-shaped. Small retinaculum present at basal third of each mandible, and a short stiff seta occurs on lateral edge of each mandible opposite retinaculum. Antennae 4-segmented, with the third and fourth articles bearing short setae and small sensory papillae. Third article with two sensory papillae apically, one laterally and one mesally, and fourth article with an apical papilla. There is no supplementary process as there is in the first two instars. Labial palpi each 2-segmented, and the venter of the labium bears two short setae. Maxillae short and stubby, each consisting of a stipes fused to the cardo. Stipes with two setae, one laterally and one ventrally. At apex of each stipes there is a 4-segmented palpus and a long thin mala. Mala and palpus both devoid of setae in this instar. Venter of head capsule with two tentorial pits near the center as in other instars. Sides of head similar to those of the second instar but with fewer pigmented granules. *Thorax*. Prothorax broader and slightly longer than head. *Legs*. Legs very short, only being about the length of head. *Abdomen*. Abdomen 10-segmented and very soft. The middle abdominal segments are expanded, each with eight lobes beneath. Urogomphi very short, unsegmented, and soft, each bearing five long setae (one basally and four actually on the urogomphus). The pygopod of the first and second instars has been entirely lost in this stage.

Fourth and fifth instar larvae (Photographs 5, 6).—These two instars look almost identical. They are 8-10 mm in length if the host pupa was *Tropisternus*, but only 6-7 mm long if they fed on the pupa of *Berosus*. The resemblance to the third instar is evident. The lack of cephalic pigment, the soft, expanded abdominal segments, and the setal arrangements on the head and body are all characteristic of all of these older instars. *Head* (Plate 3, figures 1, 2, 3, 4). Head rounded and small, as in third instar. Epicranial suture more visible than in third instar enclosing a well developed frontoclypeal area. Frons flat, rather than concave. Cervical region of head present, but short. Mandibles thick and flat, with a larger retinaculum than in third instar. Each mandible bears a lateral seta at basal third. In the last two instars the antennae become 5-segmented because of a subdivision of the original first article of younger instars. In the fourth instar the first, third, fourth and fifth articles bear short setae, one dorsally and one ventrally on first article, one mesally on third article, and four setae forming a rosette on each fourth and fifth articles. Fifth instar antenna similar, but only bears three setae in the apical rosette of the fifth segment. Antennae of both instars lack visible sensory papillae and supplementary processes. Labium still consists of two palpi, each being distinctly 2-segmented, and venter of labium with two short setae. Maxillae very short and stubby, each consisting of a fused cardo and stipes. Near the apex of each stipes is a 4-segmented palpus and a short mala. The stipes bear two setae, one laterally at middle and one ventrally at base. Mala devoid of setae in these instars, but maxillary palpus with two setae, one laterally on first segment and one laterally on third segment. Venter of head capsule with two tentorial pits near center, as in other instars. Fourth instar with organs of vision similar to those of two preceding instars, but with fewer pigmented granules.

Fifth instar with *no* pigmented granules and *no* stemmata. *Thorax*. Prothorax broader and slightly longer than head. *Legs* (Plate 3, figure 6). Legs very short, only being about the length of head. *Abdomen* (Plate 1, figure 1). Abdomen much the same as in the third instar, with similar urogomphi and with setae in the same positions.

Description of Pupa (Photograph 7).—Pupae of *B. pallidus* and *B. fidelis* typically caraboid. They have long dorsal hairs that support them while in their damp pupal chamber. Pupae white at first, then the eyes and mandibles begin to darken. Rest of the pupa yellows before emergence. Pupae with head tucked under prosternum and between retracted fore and middle legs. Antennae pass under eyes and then wrap around femora, paralleling retracted tibae. Long wing pads directed ventrally between middle and hind legs. Antennal apex, maxillary palpi, and all tarsi lie close together along ventral midline of abdomen. Head with four supraorbital setae on each side. Prothorax with a row of long setae near each edge and four short setae laterally on disc. Mesothorax and metathorax, and all abdominal segments have each two transverse rows of long setae dorsally. In addition each abdominal segment has a small, fleshy tubercle laterally (Plate 1, figure 2) and two long, thick setae and four to six short finer setae arise from each tubercle.

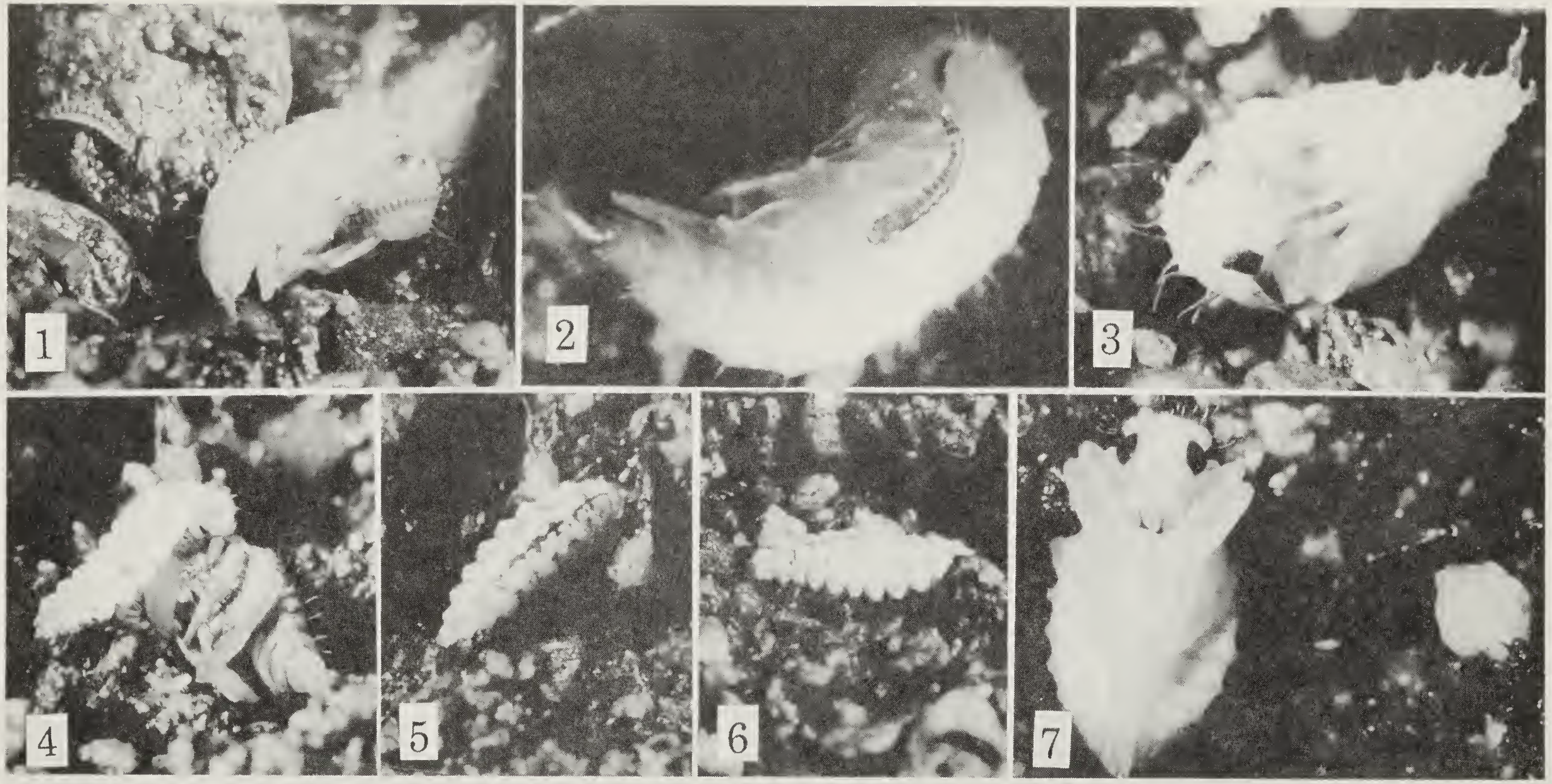
BEHAVIOR OF BRACHINUS LARVAE

The first instar *Brachinus* larva runs actively through the gravel and under algal mats near the water's edge. When it encounters a water beetle larva or pupa suitable for development, the *Brachinus* larva enters the water beetle's pupal chamber and crawls upon the pupa. The larva roams all over the pupa, using its pygopod for locomotion, but usually begins to feed on the prosternum of the host pupa. A possible reason for selecting that site may be that the pupal head is tucked under the thorax and provides a convenient place into which the larva can wedge firmly. Normally the thrashing of the pupa would be enough to throw off the parasitoid, but after it is wedged in the tight crevice between the head and the prosternum, the larva is apparently difficult to dislodge.

Larvae of *B. pallidus* have been found associated with both the pupae and larvae of *Tropisternus ellipticus* (LeConte) and with pupae of *Berosus punctatissimus* LeConte. Feeding has been observed on the pupae of both these hydrophilid beetles. In both cases adulthood was reached, but the respective *Brachinus* adults were of different sizes, probably due to the difference in size of the two kinds of hosts (these *Tropisternus* pupae are about a third larger than the *Berosus* pupae).

As many as five first instar larvae of *Brachinus pallidus* Erwin have been found on one *Tropisternus* pupa, and two first instar larvae were even found on one *Tropisternus* LARVA. One of the first instar *Brachinus* remained with the hydrophilid larva until the latter pupated, then began feeding on the pupa. In the cases where more than one first instar larva was present on a live pupa or larva, there was never any fighting or double feeding involved. All *Brachinus* larvae departed except the first individual that began feeding. One of these left-over larvae was placed on another pupa, where it soon developed into an adult, just as it normally would have on the first host encountered.

After feeding begins the young larva will sometimes leave the host pupa for brief intervals, but it always remains within the pupal chamber. Subsequent stages of *B. pallidus* larvae are generally much less active than the first instar,



PHOTOGRAPH 1. Two first instar Brachinus pallidus larvae with the pupa of Tropisternus ellipticus in the pupal chamber of the latter. PHOTOGRAPH 2. First instar of B. pallidus on pupa of T. ellipticus. PHOTOGRAPH 3. Second instar of B. pallidus on pupa of T. ellipticus. PHOTOGRAPH 4. Third instar B. pallidus on pupa of T. ellipticus. PHOTOGRAPH 5. Fourth instar of B. pallidus with remains of pupa of T. ellipticus. PHOTOGRAPH 6. Fifth instar of B. pallidus in pupal chamber of T. ellipticus after the latter was consumed. PHOTOGRAPH 7. Pupa of B. pallidus in pupal chamber of T. ellipticus.

	Host	Degenerate	Urogomphi	Claws per tarsus	Antennal segments	"parasitic"	Instars	Pygopod crochets	Urogomphi	Claws per tarsus	Ligula	Segments of outer lobe	Inner lobe present	Protheca	Retinaculum	Antennal segments
BRACHINUS	Water beetle pupae	+	+	1	5	+	5	-	+	1	-	1, 2	-	-	+	4
PHEROPSOPHUS	Mole cricket eggs	+	-	1	4	+	?	-	-	2	±	2	-	-	-	4
SPHALLOMORPHA	Ant nest	+	-	2	4	+	3	?	-	2	+	?	-	-	-	?
LEBIA	Chrysomelid pupae	+	-	2	4	+	3	-	+	2	-	2	-	+	?	4
PELECIUM	Beetle pupae or millipeds	+	?	?	?	+	?	?	?	?	?	?	?	?	?	?
ORTHOGONIUS	Termites	+	-	1	4	+	3	-	-	1	+	2	+	-	+	4
ARSINOE	Tenebrionid larvae	-	+	2	4	+	?	+	+	2	+	2	-	+	+	4
		Later instars (3 to 5)				First instar larvae										

TABLE I. Summary of characters known on "parasitic" carabid larvae; plus (+) indicates presence of listed characters; minus (-) indicates absence; numbers indicate number of segments, stages, etc.

but the second, third, and fourth instars also often leave the host for brief intervals and roam about inside the pupal chamber. If any instar (two through five) is disturbed by a touch or by strong illumination, the following characteristic reaction occurs. The larva lifts its head and thorax into the air, away from the substrate, and at the same time the abdominal apex is also elevated. This action leaves the larva resting only on the second through fifth abdominal segments, which are lobed beneath.

The fourth instar of *B. pallidus* finishes eating the water beetle pupa, devouring everything except the pronotal plate and the top of the head capsule. It then moults into the fifth instar (Plate 1, figure 1), which remains inactive during the four or five days that elapse before pupation.

An attempt was made to feed the fourth instar on another pupa after it had finished the first one, in hopes that an exceptionally large specimen might result. The second host was not eaten. Future experimentation along this line is anticipated.

RELATIONSHIPS BETWEEN BRACHINUS AND OTHER CARABIDS

Many of the characters of the larvae of *Brachinus* and of *Pheropsophus* indicate that the bombardier beetles may be only remotely related to other Carabidae. At the same time, their gross morphology indicate that they are good carabids as the family is now defined.

Among the Carabidae only the genera *Brachinus, Lebia,* and *Pelecium* are known to have ectoparasitoid larvae. *Pheropsophus* larvae are degenerate in later instars, much the same as *Brachinus,* but feed on mole cricket eggs (Habu and Sadanaga, 1964). The Pseudomorphine, *Sphallomorpha* is also degenerate, but the food source is unknown. Moore (1964) suspects it may be fed by the ants with which it lives.

The antennae of carabid larvae are usually four-segmented, except for some members of the tribe Pterostichini (including Agonini) which have five-segmented antennae and those of the tribe Anthiini which have only three segments (Hinton, 1945). *Brachinus pallidus* larvae have four antennal segments in the first three instars and five segments in the last two instars. (A subdivision of the first segment takes place during the third moult.)

The mandibles of *Brachinus* larvae are typically caraboid in all instars with a small retinaculium at the basal third, but there is no basal prostheca as found in members of the Harpalini, Elaphrini, Trechini, and Lebiini. The presence or absence of a retinaculum losses its significance at higher taxic levels in the bombardier beetles because in *Pheropsophus* it is missing.

Unlike almost all other carabids, the larva of *Brachinus pallidus* has each maxilla equipped with a one-segmented galea (here called a mala) rather than the two-segmented form which arises from the stipes of most carabids. Some European *Brachinus* and the known *Pheropsophus* have a very small first segment and a long second segment. A lacinia is absent in immature *Brachinus* as well as in those of most other Carabidae. The inner lobe of the stipes (Van Emden, 1942) is also absent. The labial palpi are two-segmented (a condition common to most carabid genera) but the ligula is entirely absent in all *Brachinus* studied. All other carabid larvae (except *Lebia scapularis* and apparently *Pheropsophus jessoensis*) that have been examined possess a ligula, although in *Pheropsophus hispanicus* and in *Sphallomorpha* it is very small. As Lindroth points out (1960:33) the ectoparasitoid mode of life is associated with a secondary loss of

the ligula. The only other carabids without a ligula are the larvae of *Trachypachus* and *Gehringia,* both of which are considered to be primitive on the basis of other criteria. Unfortunately, the food of the larvae of these genera is not yet known.

Nearly all carabids have five-segmented legs, with two claws per tarsus. The first instars of *Brachinus pallidus, nigricornis* and *incomptus* have five segments in each leg, but only one claw per tarsus. In all other instars there are only three segments, a condition found elsewhere only in the degenerate instars of *Lebia,* and *Pheropsophus. Pheropsophus* again diverts from *Brachinus* in having two claws per tarsus in the first instar.

The abdomen of *Brachinus* is 10-segmented with a pair of dorsal urogomphi on the ninth segment, a condition common to most carabid genera, but the urogomphi are unique in *Brachinus.* The first instar has short urogomphi about one-third the length of the pygopod. In later instars the urogomphi are much shorter in relation to the body length, but longer in relation to the pygopod. This holds true in *B. sensu stricto* and in *B. (Brachynidius)* and may be related to the parasitoid way of life. In *Pheropsophus, Sphallomorpha,* and *Orthogonius,* all of which have larvae which are parasitic or symboint, the urogomphi are entirely absent. In the first instar of *Brachinus* the tenth segment is tubular and serves as a pygopod, but there are no sclerotized crochets at the apex as there are in some other carabids. Instead, a pair of adhesive protrusible vesicles occurs at the apex of the pygopod of larvae of *Brachinus,* which apparently serves very well as an effective and in rapid locomotion.

The greatest differences between *Brachinus* and most other genera of carabids are in the developmental biology. In all other known carabids there are only three larval instars and the third moult releases the pupa. *Brachinus,* however, undergo five moults, with the fifth moult releasing the pupa. Van Emden (1942) suggests that perhaps the Helluonini may have more than three larval stages.

Conclusions about the phylogenetic relationships of the Brachinines must await discoveries of the immature stages of the other genera in the group, with work such as that done by Wautier (1964). The adult beetles are very closely associated with similar habitus and habits, but as I have shown here, the *Brachinus* and *Pheropsophus* larvae are quite unalike. Moore (1964) suggests that the similarities between *Sphallomorpha* and *Brachinus* at the larval level supports Jeannel's Balteifera at the adult level, that is, the concept of a separate group uniting the Pseudomorphinlae and the Brachininae. The actual characters of the larva of Moore's *Sphallomorpha* are more similar to those of *Pheropsophus,* but these apparent affinities may be a result of structural degeneration of the parasitoid larvae. Comparisons such as Moore's might have much more validity if the first instar larvae were used, rather than the degenerate later instars.

SUMMARY

A historical summary of life history information is given concerning the bombardier beetles. The life history of *Brachinus pallidus* Erwin is discussed in length and illustrated with photographs of all instars. The external morphology of all instars of *B. pallidus* larvae and pupae is described and illustrated. The behavior of these larvae is discussed in detail; and finally, relationships between *Brachinus* and other carabids are discussed. More work must be done at the larval level before true phylogenetic relationships can be established for the bombardier beetles.

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PLATE 1

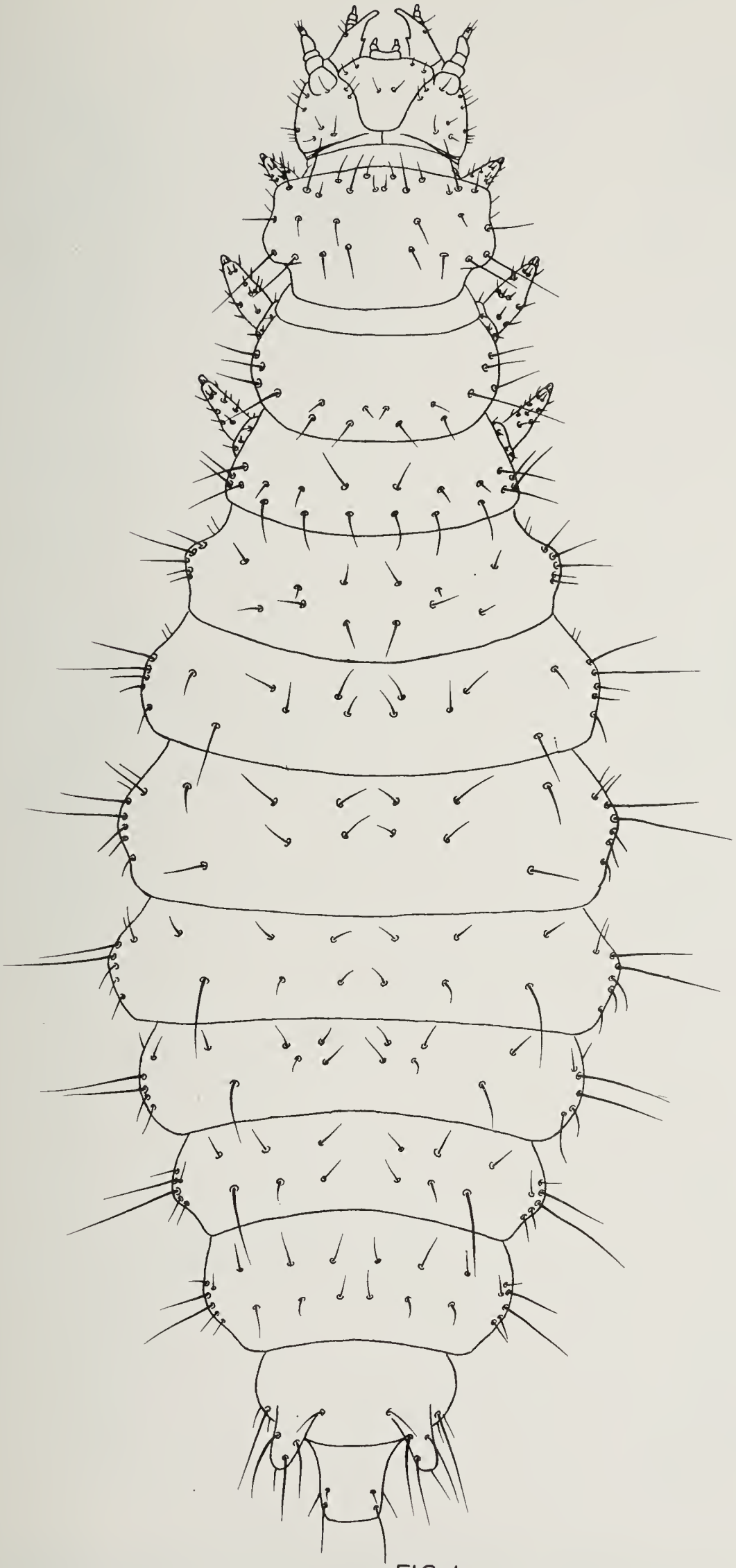
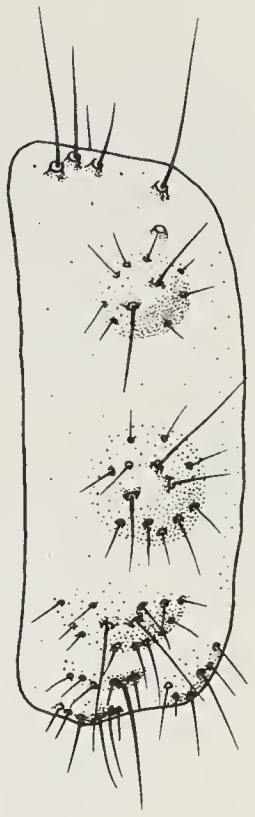


FIG. 1.



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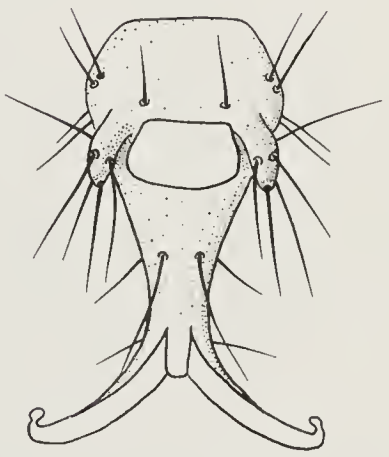
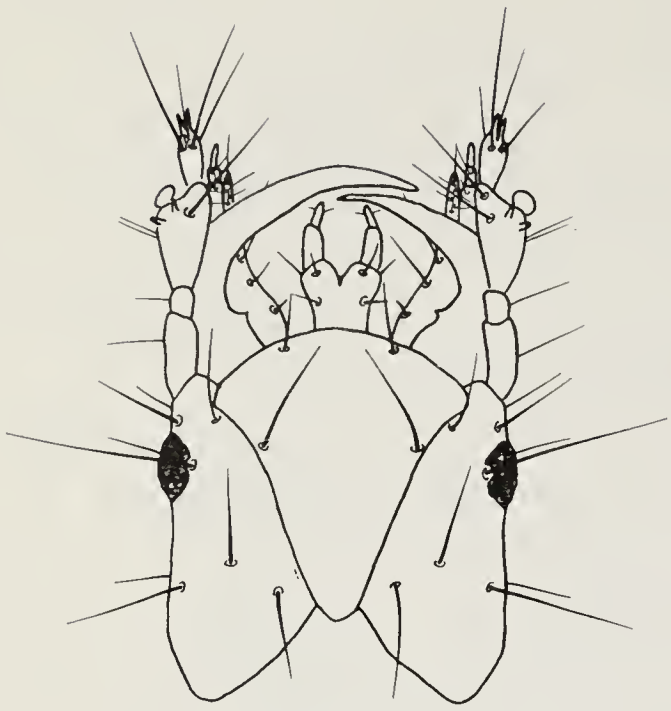


FIG. 3.

PLATE 1. *Brachinus pallidus* Erwin. FIGURE 1—Fifth instar larva from dorsal view; FIGURE 2—Lateral view of the second abdominal segment of fifth instar larva; FIGURE 3—Tenth abdominal segment of first instar larva from dorsal view.

PLATE 2



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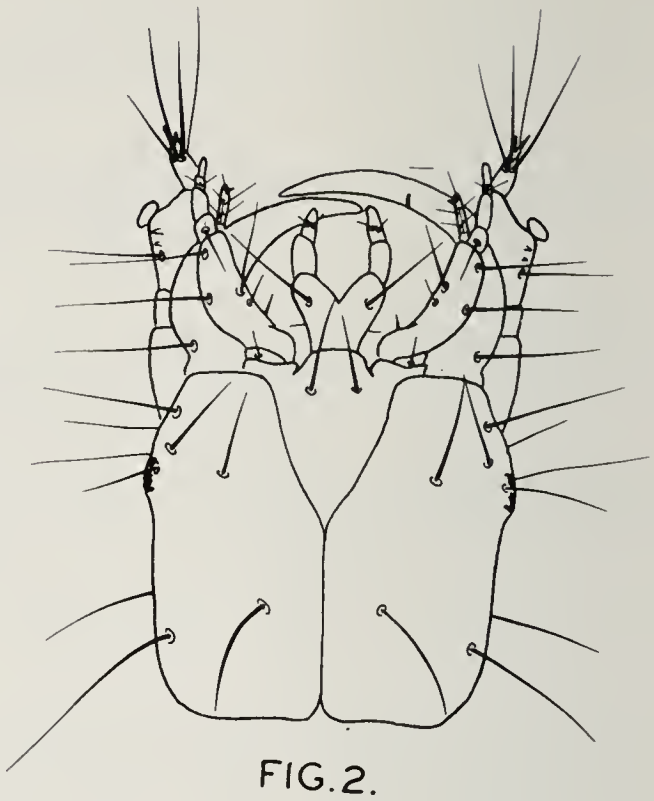
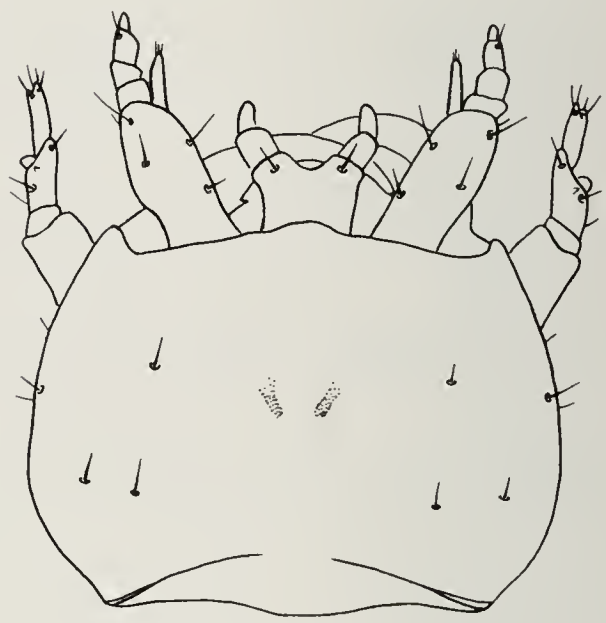


FIG. 2.

FIG. 3.



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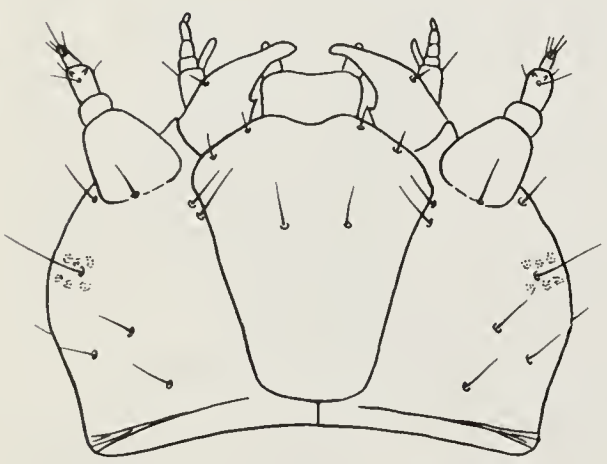

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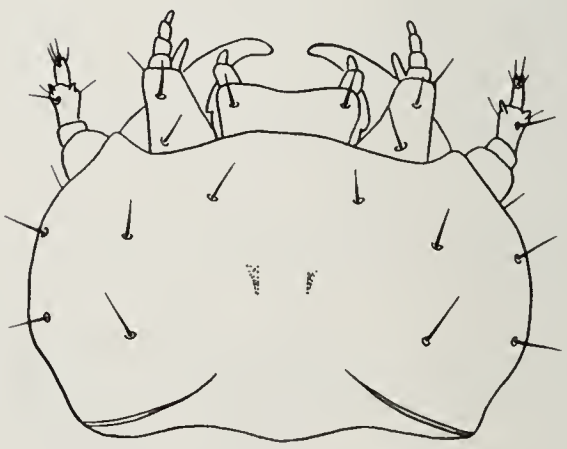


FIG. 6.

PLATE 2. *Brachinus pallidus* Erwin. FIGURE 1—Head capsule of first instar larva from dorsal view; FIGURE 2—Head capsule of first instar larva from ventral view; FIGURE 3—Head capsule of second instar larva from dorsal view; FIGURE 4—Head capsule of second instar larva from ventral view; FIGURE 5—Head capsule of third instar larva from dorsal view; FIGURE 6—Head capsule of third instar larva from ventral view.

PLATE 3

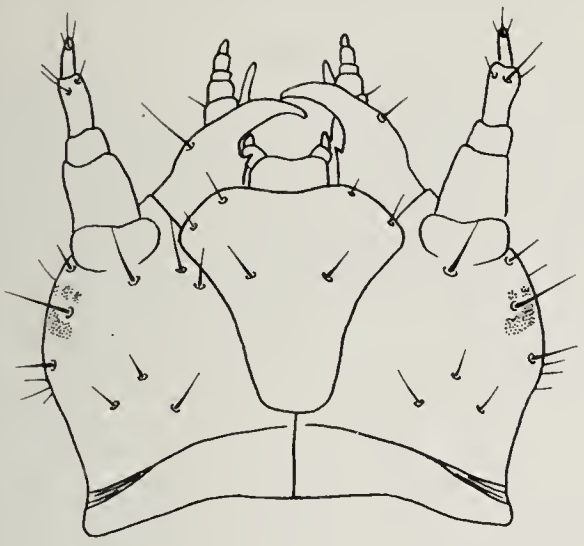
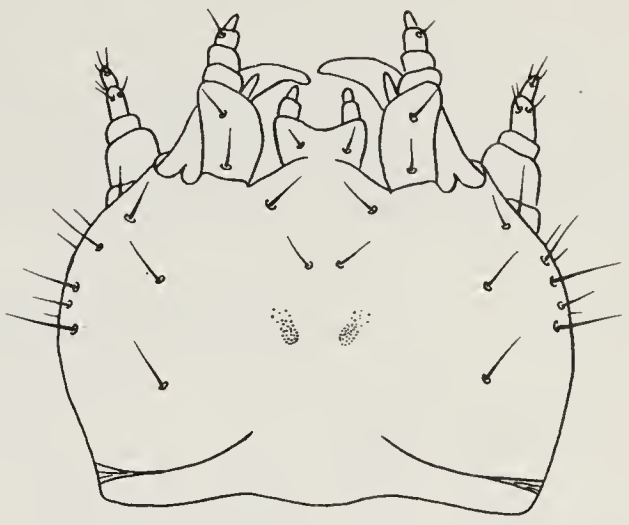


FIG. 1.



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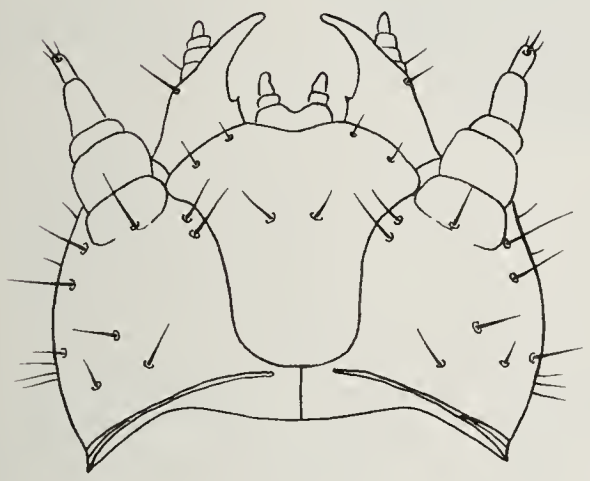

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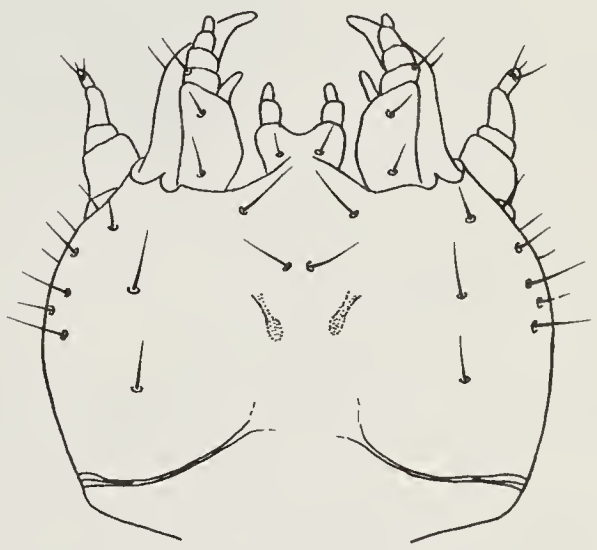
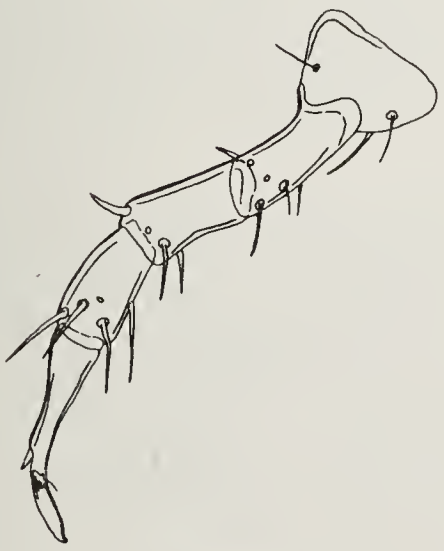


FIG. 4.



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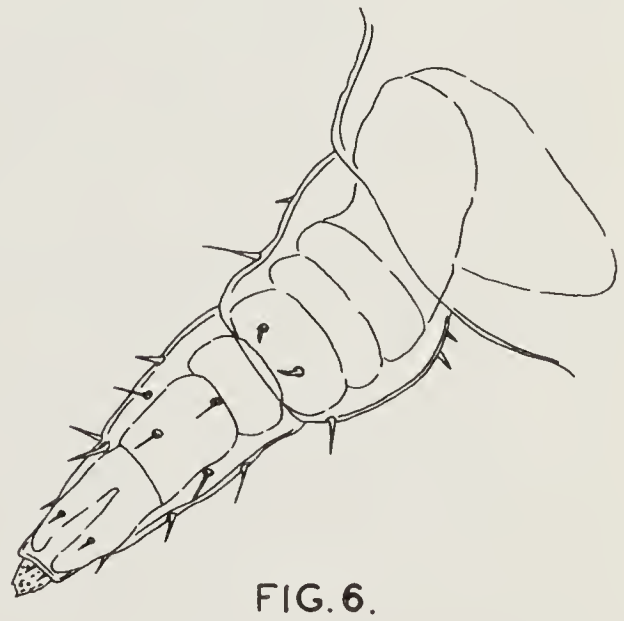

FIG. 6.

PLATE 3. *Brachinus pallidus* Erwin. FIGURE 1—Head capsule of fourth instar larva from dorsal view. FIGURE 2—Head capsule of fourth instar larva from ventral view. FIGURE 3—Head capsule of fifth instar larva from dorsal view. FIGURE 4—Head capsule of fifth instar larva from ventral view. FIGURE 5—Prothoracic leg of first instar larva from lateral view. FIGURE 6—Prothoracic leg of fifth instar larva from lateral view.